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Lateral masking in cycling displays: The relative importance of separation, flanker duration, and interstimulus interval for object-mediated updating

Elisabeth Hein[¶], Cathleen M Moore

Department of Psychology, University of Iowa, 11E Seashore Hall, Iowa City, IA 52242, USA

Abstract

A central bar repeatedly presented in alternation with two flanking bars can lead to the disappearance of the central bar. Recently it has been suggested that this masking effect could be explained by object-mediated updating: the information from the central bar is integrated into the representation of the flankers, leading not only to the disappearance of the central bar as a separate object, but also to the perception of the flankers in apparent motion between their real position and the position of the central bar. This account suggests that the visibility of the central bar should depend on the same factors as those that influence the construction and maintenance of object representations. Therefore separation between central bar and flankers should not influence visibility as long as the time interval between them is adequate to make an interpretation of the scene in terms of one object moving from one location to the other possible location. We found that if the time interval between the central bar and the flankers is neither too short nor too long, the central bar becomes invisible even at large separations. These findings are inconsistent with traditional accounts of the cycling lateral masking displays in terms of local inhibitory mechanisms.

1 Introduction

Lateral masking refers to reduced visibility of one stimulus (the target) that is caused by another spatially proximate but non-overlapping stimulus (the mask). The mask can either precede the target (paracontrast masking) or follow the target (metacounter masking) in time. A particularly striking form of lateral masking that involves both paracontrast and metacounter masking occurs when the target and masks are presented in a continuous cycle (eg Werner 1935). Figure 1 illustrates the phenomenon. A central bar is presented briefly in counterphase with two flanking bars. For a range of flanker durations, the central bar can become invisible, leaving the perception of only two flickering flanking bars. In addition to the central bar disappearing, observers often perceive inward and outward motion of the flanking bars (Hein and Moore 2010; Pilling and Gellatly 2009).

Theories of lateral masking in general range from low-level local-inhibition accounts (eg Breitmeyer and Ganz 1976; Francis 1997) to higher-level accounts that include a role for

[¶]Now at Université Paris Descartes – CNRS, 45 rue des Saints Pères, 75006 Paris, France; elisabeth.hein@parisdescartes.fr.

object representations (Duangudom et al 2007; Enns and Di Lollo 1997; for a review see Breitmeyer and Öğmen 2006). Similarly, accounts of lateral masking in cycling displays like that illustrated in figure 1 have ranged from local lateral-inhibition accounts to higher-level accounts. According to one low-level account, for example, the visibility of the central bar is reduced because the activity of neurons in early areas within the visual processing system (eg the lateral geniculate nucleus, LGN), which would normally respond to the central bar, is inhibited by activity in other neurons, also in the LGN, that respond to the spatio-temporally proximate flankers (Macknik and Livingstone 1998). Related explanations have been offered in terms of local competition for representation of border ownership (Enns 2002; Werner 1935). According to this view, the representation of the central bar cannot be established because the flankers tend to win the local competition for ownership of the shared edge between the central bar and the flankers. The flankers have an advantage because they have boundaries that are not in competition on their outer sides. As a consequence, the shared borders are represented as belonging to the flankers, and no representation of the central bar is therefore established.

An alternative account of masking in cycling displays has been offered in terms of object-mediated representational updating (Enns et al 2009; Lleras and Moore 2003; Moore and Lleras 2005; Moore et al 2007), which links the masking closely with apparent motion (Hein and Moore 2010). According to this account, the visibility of the central bar is reduced because it is represented as a previous instantiation of the flankers. As the representation of the scene is updated over time, the information that is associated with the central bar (eg its location) is integrated into the representation of the flankers, rendering the central bar invisible (see Herzog et al 2001 for related ideas about the target becoming less visible owing to perceptual grouping with the mask). As a consequence of this representational updating, motion is perceived between the central bar and the flankers [see Pilling and Gellatly (2009) for another account relating this kind of masking to apparent motion, in particular].

Local-mechanism accounts of masking of cycling displays (Enns 2002; Macknik et al 2000; Werner 1935) predict that the visibility of the central bar will depend on the close proximity of borders between the central bar and the two flankers. In contrast, the object-mediated updating account (Hein and Moore 2010) predicts that, as long as the central bar and the flankers are within sufficient range spatially and temporally to support the perception of apparent motion (Attneave and Block 1973; Korte 1915; Neuhaus 1930), visibility of the central bar should be reduced. Several studies have manipulated the distance between the central bar and the flankers in cycling displays (Enns 2002; Hein and Moore 2010; Macknik et al 2000; Werner 1935). Macknik et al (2000), for example, found that single-cell responses in monkey LGN showed decreasing inhibition as the central bar and the flankers were spatially separated from each other. In humans, Enns (2002) showed that visibility ratings of the central bar increased with increasing separation between the central bar and the flankers, at least within a range of very small separations (0.07 to 0.13 deg or 2 to 4 pixels). Finally, using a range of much larger separations, Hein and Moore also found a decrease of visibility ratings of the central bar with increasing separation. Critically, however, visibility of the central bar, which was presented at an eccentricity of about 1.3 deg above and below a central fixation point, was substantially reduced at all separations. Even

the largest separations (1.98 deg) yielded a substantial 43% reduction in visibility. Moreover, in a second experiment, when the flanking bars were completely separated from the central bar by displacing them vertically relative to the position of the central bar, now presented 3.0 deg to the left and right of fixation, a 42% reduction in visibility still occurred at the largest vertical separation.

Thus, on the one hand, the results from the literature are consistent with local inhibitory accounts because visibility has been found to increase with increasing separation. On the other hand, they are also consistent with the object-mediated updating account because visibility is still substantially reduced even at extreme separations, such as vertical displacement, where local competition is unlikely but apparent motion is still perceived. Of course, the two alternative accounts are not mutually exclusive. Therefore, the mixed pattern of results might reflect contributions of both local inhibitory mechanisms and object-mediated updating mechanisms. One particular possibility is that, when the separation of the central bar and the flankers is small, they inhibit each other, whereas at larger separations only object updating occurs.

In the current study we explored the link between conditions suitable for motion perception (indicating that object updating happens) and masking in cycling displays further by asking whether the reduction in masking with increased spatial separation is less if the time between stimuli changes in a manner that is commensurate with the changing spatial separation. The stimulus onset asynchrony (SOA) at which smooth motion is most effectively perceived between two stimuli depends on the spatial separation between them (eg Attneave and Block 1973; Korte 1915; Neuhaus 1930). The larger the separation between two stimuli, the longer the SOA must be to support the perception of smooth motion between them. Extending that relationship to the object-mediated updating account of masking in cycling displays, some interstimulus interval (ISI) and spatial-separation combinations may support the representation of the central bar and flankers as different instantiations of the same object better than others. Hein and Moore (2010) used a large range of spatial separations, but the central bar and flankers always followed each other immediately (0 ms ISI). That ISI might have been too short to combine effectively with the larger separations, causing the combined object representation to break down. In such a case, masking would be reduced not because of the separation per se, but because the combination of the separation and the time between the stimuli was inconsistent with a combined object representation of central bar and flankers.

We conducted two experiments in which we manipulated the spatial separation between the central bar and the flankers as well as the ISI between them. In experiment 1 we manipulated ISI from 0 to 80 ms, and in experiment 2 we manipulated ISI from 100 to 300 ms. The object-updating hypothesis predicts that, with a certain range of ISIs, larger spatial separations will have to be paired with longer ISIs in order to achieve maximal masking (ie most decreased visibility). The idea is that, as spatial separation becomes large, more time is needed to support the perceptual interpretation of an object moving from one location to another. If the central bar and flankers are not represented as a common object, then the information sampled from the central bar will not be used to update the representation of the flankers, and the central bar will therefore become visible as a separate and distinct object in

the display and no motion will be perceived. These predictions hold only for a limited range of separations and ISIs because, at a certain point, the ISI will become too long for object updating, and as a consequence motion and masking to occur, regardless of the mechanism.

By way of preview, experiment 1 revealed exactly the pattern of results predicted by an object-mediated updating account of masking in cycling displays. The longer the ISI between the central bar and the flankers, the less visible was the central bar and, critically, the less visibility depended on separation. Moreover, in experiment 2 when the ISI became even longer, visibility of the central bar increased again, the two experiments together showing the expected U-shaped function of apparent motion and masking with ISI.

2 General method

2.1 Participants

Five observers participated in experiment 1 (mean age 25 years, two females) and a different set of five observers in experiment 2 (mean age 21 years, three females). They were all naive as to the purpose of the experiment. Observers received either course credit for their participation or were paid \$24 to compensate for their time. All participants reported normal or corrected-to-normal visual acuity and normal color vision.

2.2 Apparatus

The experiment was controlled by a Macintosh computer (Mac OS X, Version 10.4.10) driving a 17-inch color CRT monitor with a spatial resolution of 1024×768 and a refresh rate of 100 Hz. Stimuli were presented on the screen with MATLAB software (version 7.4 release 2007a; Mathworks, MA) in combination with the Psychophysics Toolbox extensions (version 3.0.8, flavor beta—Brainard 1997; Pelli 1997). Viewing distance was fixed at 60 cm with a chin-and-head rest.

2.3 Stimuli

Each masking display consisted of a set of three individual black (0.5 cd m^{-2}) bars, each being 3.0 deg high and 0.6 deg wide, presented on a mid-gray background (40.1 cd m^{-2}). Following Enns (2002) we presented two identical sets of masking displays in order to encourage participants to remain fixated in the center. The displays were presented 1.3 deg above and below a black central fixation cross ($0.4 \text{ deg} \times 0.4 \text{ deg}$). To prevent the two displays forming a line with fixation, the upper display was displaced 0.3 deg to the right of the midline and the lower display 0.3 deg to the left. The central bar of each display always stayed at the same position, but the flankers were presented at seven different positions, either directly next to the central bar or at a distance of 0.06, 0.12, 0.25, 0.50, 0.99, and 1.98 deg (2, 4, 8, 16, 32, or 64 pixels) between the border of the central bar and the flankers. The experiments were conducted with regular room lights put on low.

2.4 Task

Participants had to judge the visibility of the central bar, using one of seven possible keys ('1' to '7' on the central keyboard). Participants were instructed to press the '1' key when the central bar was invisible, and the '7' key whenever the central bar was entirely visible,

and any key in-between according to how visible the central bar appeared to them. Participants were informed that they could base their judgment on either of the masking displays or both of them, as they would always be identical.

2.5 Design

A 4 (flanker duration) $\times$ 7 (separation) $\times$ 6 (interstimulus interval) within-subjects design was used. The different factors were counterbalanced and mixed within blocks of trials. Each observer completed three experimental sessions with 336 trials each on separate days. Overall, we collected six observations for each condition for each participant.

2.6 Procedure

In the beginning of each session a set of written instructions describing the task was presented on the computer screen. After reading the instructions, observers were shown two extreme examples of the display at separation 0, in which the central bar was either completely visible (at a flanker duration of 20 ms) or invisible (at a flanker duration of 300 ms). The experimenter emphasized the importance of remaining fixated on the central fixation cross and participants were encouraged to refixate before judging visibility of the central bar in case they had lost fixation. Every 36 trials a break was provided, and observers were encouraged to rest as much as they needed during these breaks. The next block could be initiated at any time by pressing a button on the keyboard. Each experimental session lasted about 45 min.

Trial events are illustrated in figure 2. Each trial began with the presentation of the central fixation cross. After fixating, participants pressed the space bar to start the trial. Two sets of flankers appeared above and below fixation, presented for different flanker durations of either 20, 70, 110, or 300 ms. After a variable ISI of either 0, 10, 20, 40, 60, or 80 ms in experiment 1, and 100, 120, 160, 200, 250, or 300 ms in experiment 2 the central bar was always presented for 100 ms. The central bar was then followed by the same ISI, before the flankers were presented again. The central bar and the flankers were presented in alternation until the participants responded or at least for 1.5 s (the central fixation cross became thicker in order to indicate that this period was over and a response could be given). An intertrial interval of 500 ms separated consecutive trials. If participants responded too early, or used a different key than one of the seven response keys, an error message appeared on the screen. These trials were repeated at the end of each block.

3 Results and discussion

Mean group responses for individual observers were submitted to a 4 (flanker duration) $\times$ 7 (separation) $\times$ 6 (interstimulus interval, ISI) analysis of variance (ANOVA). In this and all following analyses α was set at 0.05 and p -values were Greenhouse – Geisser corrected to adjust for violations of the sphericity assumption.

Figure 3 shows mean visibility ratings from experiment 1 as a function of ISI, flanker duration and separation for experiment 1, in which ISIs from 0 to 80 ms were used. There were reliable main effects of flanker duration ($F_{3, 12} = 32.33, p < 0.001$), and ISI ($F_{5, 20} = 14.86, p < 0.05$), as well as an interaction between these two factors ($F_{15, 60} = 12.30, p <$

0.01). Visibility ratings decreased, ie the central bar became less visible, as both flanker duration and the ISI increased. In addition, visibility ratings were affected less by flanker duration as ISI increased, whereas visibility ratings for the shortest ISI varied a lot with flanker duration, ranging from a visibility rating of about 6.5 to 2 (as can be seen in figure 3, comparing the average ratings at an ISI of 0 for each of the four flanker-duration conditions); at the longest ISI, on the other hand, visibility was low at all flanker durations, ranging from a visibility rating of about 3.5 to 2 (visibility rating for all but the shortest flanker duration being at about 2). As in previous studies (eg Enns 2002; Hein and Moore, 2010) there was also a main effect of separation ($F_{6, 24} = 9.54, p < 0.05$). However, LSD a-posteriori comparisons revealed that the only reliable differences were between the largest separation (1.98 deg) compared to all other separations, and the second to largest separation (0.99 deg) compared to the two smallest separations (0 and 0.06 deg). Furthermore and most relevant to the question addressed in this study, there was a reliable interaction between ISI and separation ($F_{30, 120} = 5.02, p < 0.05$). As can be seen in figure 3 by looking at how the individual curves come together closer and closer (for each flanker-duration condition), the longer the ISI, the less influence separation had on visibility ratings. In particular, at the longest ISI visibility was very low (around 2.2) for all but the largest separation. In contrast, for the shortest ISI condition visibility ratings varied from about 5.2 to 3.2 from the largest to the smallest separation. As can be seen in the steepness of the individual separation curves in figure 3, the larger the separation between the central bar and the flankers, the longer the ISI needed to be for visibility ratings to come down.

Figure 4 shows mean visibility ratings from experiment 2, in which ISI varied from 100 ms to 300 ms, as a function of separation, flanker duration, and ISI. There were again reliable main effects of flanker duration ($F_{3, 12} = 61.21, p < 0.001$) and ISI ($F_{5, 20} = 13.29, p < 0.05$), and an interaction between them ($F_{15, 60} = 4.79, p < 0.05$). In this case, however, the central bar became more visible, not less visible, as flanker duration and ISI increased. Moreover, even though there was still an interaction between flanker duration and ISI in this experiment as compared to experiment 1, it was less pronounced, visibility ratings ranging from about 2.7 to 5.3 (shortest to longest flanker duration) at the shortest ISI condition and 3.9 to 6.0 at the longest ISI condition. Finally, there was again a reliable main effect of separation ($F_{6, 24} = 14.65, p < 0.05$), but no significant interaction between ISI and separation ($F_{30, 120} = 0.90, ns$). As the separation between the central bar and the flankers as well as the ISI increased, the more visible the central bar became. LSD a-posteriori comparisons revealed that all but the first three separations (0 to 0.12 deg) were significantly different from each other. In contrast to experiment 1, however, the increase in visibility with increasing ISI and separation was very similar for each separation condition, even though the pattern of results looks pretty similar to the one of experiment 1 (especially if one compares the parallelism of the different separation curves for the shortest flanker duration with the merging of the curves at the largest flanker duration).

In experiment 2, visibility of the target tended to increase with increasing flanker duration, whereas the opposite occurred in experiment 1. Notice, however, that increasing flanker duration leads to an increase in the SOA between the flankers and the central bar. This means for experiment 2 that the longer the flanker duration, like the longer the ISI itself, the less likely is the apparent motion perceived, and therefore the less likely is the representation

of the central bar updated with the representation of the flankers, making the central bar more likely to be visible.

Together, the results of experiments 1 and 2 showed that the dependence of visibility on separation strongly depends on ISI, thereby supporting the object-mediated updating account of masking in cycling displays. In particular, as could be seen in experiment 1, the larger the separation between central bar and flankers became, the longer the ISI needed to be in order to produce low visibility of the central bar. These results are consistent with what would be expected in terms of suitable condition for perceiving apparent motion between the central bar and the flankers: the larger the separation between two objects, the longer the time interval between them needs to be in order to perceive good apparent motion (eg Korte 1915). At long ISIs the visibility of the central bar was substantially reduced even in conditions in which the duration of the flankers was only a fifth of the duration of the target and in which at short ISIs the central bar was completely visible. Furthermore, as the ISI became too long, visibility of the central bar increased again, as was shown in experiment 2, leading to a U-shaped function that is well known in masking (eg Fehrer and Smith 1962; Growney et al 1977; Kolers 1962; Schiller and Smith 1966) and the apparent motion (eg Kahneman 1967; Korte 1915) literature when both experiments are taken together.

4 General discussion

The aim of this study was to test a prediction of the object-updating account of masking in cycling displays that was proposed by Hein and Moore (2010). According to this account, the central bar is rendered invisible because the flanking bars are represented as later instantiations of the central bar. As a consequence, stimulus information from the central bar is integrated with the representation of the flankers and is not therefore perceived distinct from them (see Herzog et al 2001, for a similar idea on how grouping of target and mask can reduce the visibility of the target). The manifestation of the central bar in the overall percept is in the form of perceived inward and outward motion of the flankers. This idea is based on the proposal that the process of updating representations of dynamic scenes is mediated through object representations (eg Enns et al 2009; Lleras and Moore 2003; Moore and Enns 2004; Moore and Lleras 2005; Moore et al 2007). To the extent that newly sampled information is perceived as deriving from an object for which a representation already exists, the representation of that object will be updated on the basis of that information. If, however, newly sampled information is perceived as deriving from a different object, then the original object representation will be 'spared' from updating and will remain visible in its most recently represented form. Under this view, how a scene is changed on the basis of newly sampled information depends on the perceived organization of the scene, which in turn, is determined by a large number of factors including, for example, feature similarity and common fate. As applied to masking in cycling displays, the idea is that, if the spatial separation and interval between stimuli are consistent with an object (the central bar) moving and in this case splitting in two new locations, then the information from the two new stimuli will overwrite (update) the information that had been represented from the central bar, rendering it perceptually inaccessible. An expected, concomitant perception in this case is that motion will be perceived between the position of the flankers and the position of the central bar. This percept has been documented in previous studies (Hein and

Moore, 2010; Pilling and Gellatly 2009). If, however, the spatial separation and/or the interval between the stimuli are inconsistent with an object moving (eg ISI is too short or too long), then the central bar will be represented as a distinct object that will not be updated on the basis of the new information sampled from the flankers. The pattern of central-bar visibility as a function of both spatial separation and ISI between it and the flankers that was reported by subjects in these two experiments is consistent with these predictions.

The object-updating account of masking in cycling displays is different from previous accounts in that it does not depend on the close proximity of the borders of the central bar and flankers (Enns 2002; Macknik and Livingstone 1998; Werner 1935). These accounts propose that the decrease in visibility is caused by local competition between the borders of the two sets of stimuli. Of course, both local competition and object updating may well play a role in reduced visibility of the central bar. Even when the central bar and the flanking bars are perceived as distinct objects, lateral inhibitory mechanisms may well act to reduce the visibility of stimuli. The point that we wish to make is that, even under conditions that render local inhibitory mechanisms irrelevant, substantial masking can occur. We suggest that this is because, when stimuli are perceived as later instantiations of already represented objects, online representational updating serves to overwrite the previous versions of those objects, rendering those previous versions perceptually inaccessible.

The object-updating account of masking in cycling displays highlights a link between apparent motion and masking that is reminiscent of an earlier debate in the literature regarding the identity between apparent motion and metacontrast masking. Some studies reported strong correlations between perceived apparent motion and metacontrast masking, suggesting that they reflected identical mechanisms (eg Bischof and Di Lollo 1995; Didner and Sperling 1980; Di Lollo et al 1993; Fehrer 1966; Kahneman 1967). In contrast, other studies led to the conclusion that apparent motion and metacontrast masking reflect at least partially different mechanisms, because the spatio-temporal conditions under which optimal masking and perceived apparent motion were observed were not the same (eg Breitmeyer and Horman 1981; Stoper and Banffy 1977; Weisstein and Growney 1969). These results imply that apparent motion and masking are not identical but might share a common mechanism (eg Breitmeyer et al 1974, 1976). In our view, metacontrast masking, like the masking in cycling displays studied here, and motion perception are correlated because they both reflect the perceptual organization of multiple stimuli as single objects; they are different instantiations of the same object at different times. Such an organization will lead both to the perception of that object moving, if the stimuli appear at different locations, and to online updating that overwrites previous versions of the object representation, rendering them perceptually inaccessible. Thus, under this view, apparent motion and masking are not identical, but are strongly related and the common mechanism that relates them is object updating.

Thus, one consequence of object updating is the suppression of the representation of the central bar and the perception of apparent motion. Another consequence would be that information other than location that is associated with the central bar, eg its shape and surface attributes, is not lost, but gets combined with the representation of the flankers or transposed to the flankers, a phenomenon known as feature inheritance or transposition in

the masking literature (eg Herzog and Koch 2001). Some observations of Werner (1935), as well as Enns (2002) suggest that this may indeed occur in cycling paracontrast and metacontrast displays as used in this study as well. Werner (1935), for example, reported that radiating spokes that are part of the central stimulus could be perceived as part of the flanker stimulus. Similarly, Enns (2002) reported that observers sometimes perceived the surface pattern of the central bar as being superimposed on the flankers. Breitmeyer et al (2008) recently suggested that the strength of feature inheritance may be determined by the strength of apparent motion. This conclusion fits well with those of the present study in that object updating, which is likely to be strongest under those conditions in which apparent motion is strongest, can result in both the kind of masking one observes in these cycling displays and feature inheritance.

In summary, we propose that masking in cycling displays can be best understood in terms of online representational updating that is mediated through object representations. This account provides an explanation for the dependence of masking in these displays on spatial separation, flanker duration, and ISI. It also accounts for the concomitant percept of inward and outward motion of the flankers (Hein and Moore 2010; Pilling and Gellatly 2009). In addition, it is consistent with the observation that the masking of the central bar is stronger when the flanking bars and central bar are similar to each other than when they are quite distinct (Enns 2002; Werner 1935). Finally, the documented influence of perceptual organization and attention on target visibility in both standard metacontrast masking (Ramachandran and Cobb 1995) and masking in cycling displays (Werner 1935) lends further credence to this explanation.

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Figure 1.

Illustration of the cycling lateral masking displays used in experiments 1 and 2. (a) The presentation of the stimuli at an interstimulus interval of 0 ms and a medium separation between central bar and flankers. (b) The resulting motion perception when the central stimulus is invisible. The arrows indicate the direction in which apparent motion is seen.

Figure 2.

Basic trial sequence in both experiments. After the participant initiated the trial, the central bar and flankers are presented in alternation until the response is given, indicating how visible the central bar appeared. This example shows a zero separation condition.

Figure 3.

Mean visibility ratings (on a scale from 1 to 7, where 1 is invisible and 7 maximally visible) as a function of ISI (interstimulus interval) and separation (horizontal distance between the sides of the central bars and the corresponding flankers) for experiment 1. Flanker presentation time (ms): (a) 20, (b) 70, (c) 110, (d) 300. Error bars indicate ± 1 SEM.

Figure 4.

Mean visibility ratings (on a scale from 1 to 7, where 1 is invisible and 7 maximally visible) as a function of ISI (interstimulus interval) and separation (horizontal distance between the sides of the central bars and the corresponding flankers) for experiment 2. Flanker presentation time (ms): (a) 20, (b) 70, (c) 110, (d) 300. Error bars indicate ± 1 SEM.